

APPARENT ECOTYPIC DIFFERENCES  
IN THE WATER RELATIONS OF  
SOME NORTHERN BOG ERICACEAE<sup>1</sup>

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The apparent paradox of xeromorphy in northern bog plants has become a popular subject again, this time however, with a new interpretation. The development of sclerophyllous leaf tissue (increased cutinization and lignification, increased fiber/protein ratio) in plants of both wet and dry habitats has recently been linked with phosphorous deficient soils (Beadle, 1966; Loveless, 1962), a feature that both deserts and northern bogs have in common. In the light of this discovery, leaf sclerophylly and the evergreen habit often associated with it are now being interpreted as reflecting a specialized metabolism tolerant of low nutrient levels, though the physiology of this adaptation is not yet fully understood (Small, 1972a, 1972b; Beadle, 1968, 1966; Monk, 1966; Loveless, 1962).

From a morphological viewpoint much of the northern bog flora seems particularly well adapted for the conservation of water. Narrow, leathery, and heavily cutinized leaves with revolute margins and vertical orientation, characters typical of many Ericaceae, are perfect water conserving adaptations. Yet these features cannot be explained on the basis of plant-water relations in the northern sphagnum bog. Early hypotheses relating these xeromorphic characters to a condition of "physiological drought," for reasons mostly associated with the anaerobic bog substrate, were dismissed long ago by Caughey (1945) for lack of experimental confirmation. More recent *in situ* determinations of the water status of bog plants by Small (1972a) and

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Marchand (1972) have likewise failed to turn up any evidence of water stress in the bog environment. While normal midday xylem water potentials in several species have been found to be quite low ( $-15$  to  $-20$  bars), stomatal response appears to be unaffected in this range (Small, 1972a; Marchand, 1972). Assuming that stomatal functioning is an adequate measure of plant sensitivity to its environment, there seems enough justification indeed to abandon our ideas of water stress in bogs.

This is not to suggest, however, that the subject of water relations of bog plants is closed. To the contrary, the acid and waterlogged substrate of the sphagnum bog poses some unique ecological problems, and the data of Small (1972a), as well as that of Marchand (1972), invite further investigation into possible differences in the water metabolism of bog plants and their counterparts on well drained sites. Specifically, the following questions may be asked: Why are xylem potentials of small bog shrubs so low, sometimes exceeding  $-20$  bars, when soil water supply in this habitat is seemingly unlimited? In an environment where soil-water supply is more restricted, how low a water potential might these species tolerate, before stomatal closure is induced? Do the observed water potentials represent an optimum "operational" level for the species in question or is the level induced by some edaphic characteristic of the habitat? Presented here are some field observations which suggest possible answers to these questions.

#### METHODS

The Lee Hill Bog in Lee, New Hampshire, is typical of northern sphagnum peat bogs, supporting a flora dominated by several members of the family Ericaceae along with *Picea mariana* (Mill.) BSP. and *Eriophorum virginicum* L. Because the bog is situated in a kettle amidst glacial deposits, however, the surrounding upland area contrasts abruptly in both edaphic character and floristic composition. Around the perimeter of the bog, the well-drained till sup-



ports a "mesic" pine-oak community. Both the bog and adjacent upland sites, however, support well established populations of *Vaccinium corymbosum* L. and *Gaylussacia baccata* (Wang.) K. Koch, thus affording an opportunity to study simultaneously the water relations of these species under similar atmospheric conditions but under markedly different edaphic conditions. In Wolcott, Vermont, a somewhat similar situation exists in which the water status of *Ledum groenlandicum* Oeder and *Kalmia angustifolia* L. growing in a wet peat substrate was compared with that of the same species growing in a well-drained upland field.

At each site, xylem potentials were measured using a portable pressure bomb (PMS Instruments Co.) as described by Waring and Cleary (1967). The pressure bomb is designed to measure the amount of tension in the xylem water column resulting from transpirational "pull" against flow resistances in the soil-plant continuum. This xylem tension is related to the free energy of the water in the plant, the water potential. When the stem of a transpiring plant is cut, the cohesion of the water column is broken and the tension is relaxed. The water column then quickly recedes from the cut surface. By placing the branchlet into a sealed chamber with only the cut end protruding, and applying pressure, the water column can be forced back to the cut surface, thus re-establishing the initial condition. The amount of pressure required to do this is equal in absolute value to the initial xylem tension or water potential of the plant.

In this study, exposed branchlets about 10 cm. in length and bearing several leaves were used for the water potential determinations. The sample number ranged from just three stems per species when variation was low, as during the early morning hours, to six when the variation within species was higher. At the time of sampling, soil-water potentials were determined using a tensiometer (Soilmoisture Equipment Corp. No. 2900) and wet- and dry-bulb temperatures were recorded with a sling psychrometer.



Since pressure bomb measurements by themselves are difficult to interpret, stomatal response to the observed water potentials was measured with a diffusion porometer. This instrument is essentially an electric hygrometer whose resistance varies inversely with humidity. In use, a small plexiglass chamber containing a hygroscopic element is clamped onto a leaf and, in effect, the leaf is allowed to transpire under prescribed conditions. As water vapor diffuses into the initially dry chamber, the time rate of humidity increase over a narrow range is noted. From this, the diffusion resistance of the leaf, mostly a function of stomatal aperture, is calculated based on a calibration curve for known resistances.

The porometer used in this study was modified from the design of Kanemasu *et al.* (1969). In order to increase instrument sensitivity for use on very small leaves the chamber volume was reduced slightly, a higher sensitivity element (Hygrodynamics No. 4-4816K) was used, and the cup aperture was reduced to 6.35 mm. diameter. With these modifications, the time required for attachment and measurement on the leaf was usually of the order of 5 to 15 seconds when the stomates were fully open. In calibration, storage, and field use, the recommendations of Morrow and Slatyer (1971a, 1971b) were followed closely.

#### RESULTS

The data from the different sites are compared by using the model of Elfving *et al.* (1972) where transpiration is described by the ratio of vapor pressure deficit (VPD) to stomatal diffusion resistance ( $r_s$ ). A plot of xylem water potential against  $VPD/r_s$  for the species studied here indicates that for any given transpiration rate, under non-stress conditions, xylem potentials are lower (more negative) in the bog plants than in their upland counterparts (Fig. 1).

The rapid development of a very steep water potential gradient in the bog plants was observed early in the day. At the Lee Hill Bog, where soil water potential was zero bars,



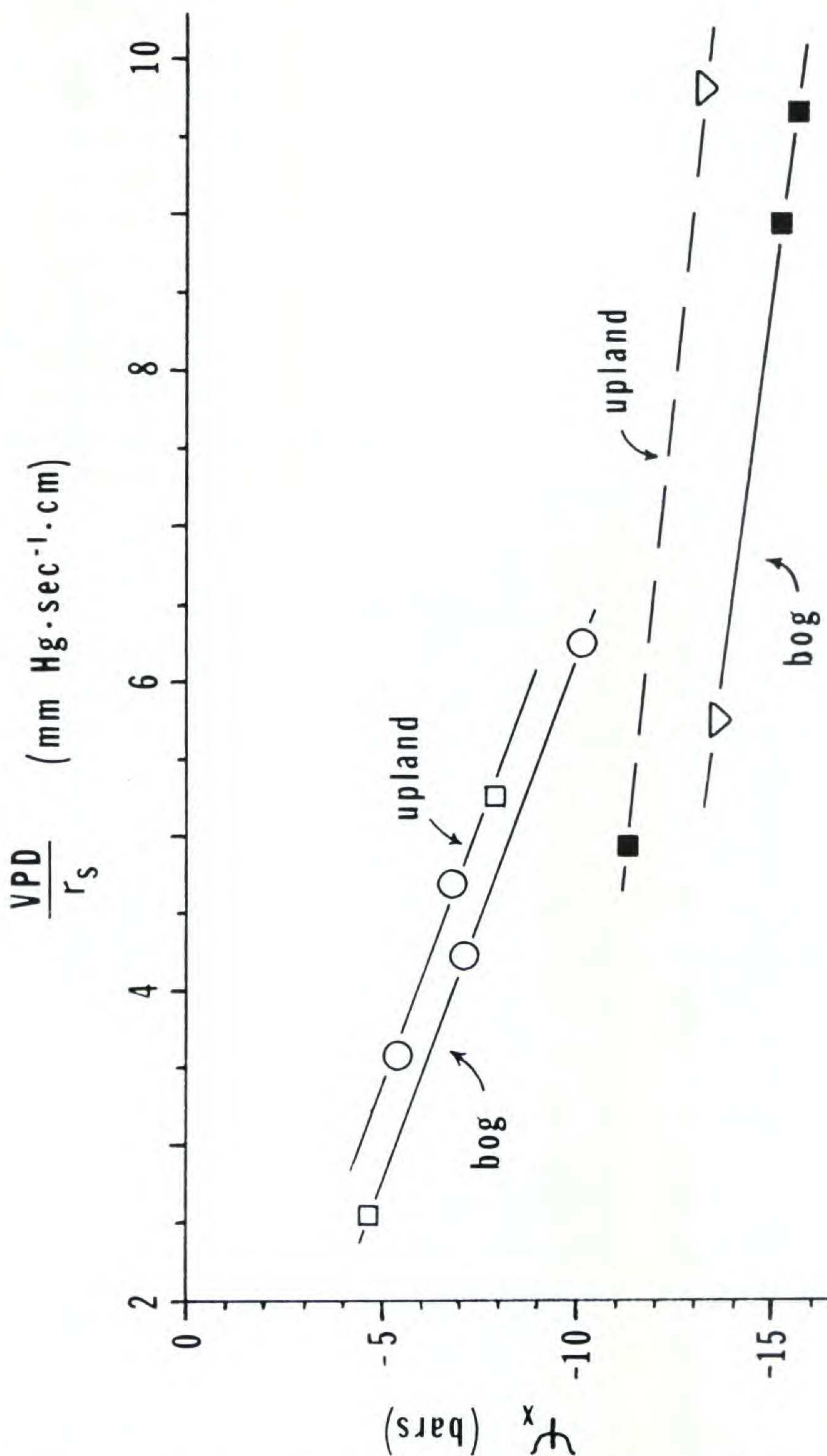


Figure 1. Xylem water potential ( $\psi_x$ ) as a function of estimated transpiration rate ( $VPD/r_s$ ) for bog and upland ecotypes under non-stress conditions. Symbols: ○ *L. groenlandicum*; □ *K. angustifolia*; ■ *G. baccata*; ▽ *corymbosum*.



transpiration from *Gaylussacia baccata* was inhibited during the first hours after sunrise by a heavy dew formation on the leaves. As soon as the dew evaporated and transpiration began, a very steep gradient was established with xylem water potential decreasing from  $-1$  to  $-15$  bars within one hour and further decreasing to  $-22$  bars in the next four hours (Fig. 2). The leaf stomates remained open ( $r_s = 1.1$  sec./cm.) throughout the day however. In the drier upland habitat where soil water potential was  $-0.3$  bars, transpiration from *G. baccata* began at sunrise with xylem water potentials decreasing gradually, eventually to be checked by an increase in stomatal resistance to an average of  $4.8$  sec./cm. by mid-morning and  $8.3$  sec./cm. by mid-afternoon (Fig. 2).

While a soil-water potential of  $-0.3$  bars is not usually considered very dry, the difference in soil-water availability between the above two sites is best indicated by the slow rate of recovery or increase of xylem potential in the upland population as compared to that of the bog population, beginning with the approach of sunset and continuing to daybreak (Fig. 2). In spite of such differences in soil-water availability, stomatal behavior, and transpiration rate (an increase in  $r_s$  from  $1.1$  sec./cm. to  $8.3$  sec./cm. is enough to cause a five-fold decrease in the transpiration rate), the mid-day depression of water potential in both populations was similar:  $-19.4 \pm 2.8$  bars in the upland population and  $-22.0 \pm 2.7$  bars in the bog population (Fig. 2).

#### DISCUSSION

When the rate of movement of water through the plant falls behind the rate of transpiration loss at the leaf surfaces, due either to internal resistances to flow or an insufficient soil-water supply, the result is a decrease in plant water potential. If there were no internal resistances in the plant, then in any situation where soil-water is non-limiting, the plant water potential would always be very high (near zero). Conversely, where soil-water is freely



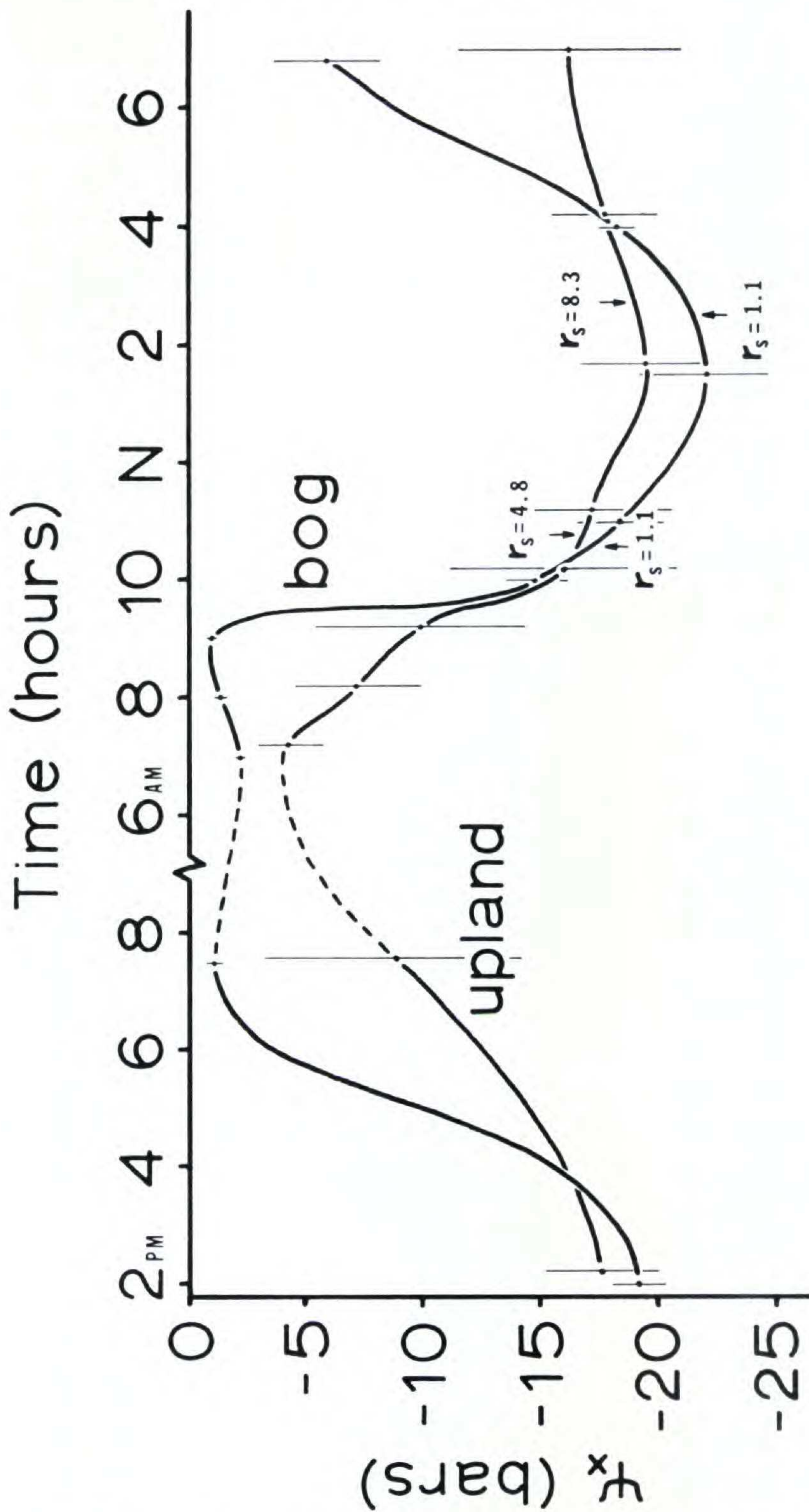


Figure 2. Diurnal trend of xylem water potential ( $\psi_x$ ) in *Gaylussacia baccata*, Lee Hill Bog and adjacent south-facing hillside. Stomatal diffusion resistance ( $r_s$ ) is given in sec./cm. Vertical bars represent standard deviations.



available and xylem water potentials become appreciably low (more negative), as in the bog community, then internal resistances are indicated.

For steady-state flow through the plant, the transpiration flux is considered to be directly proportional to the water potential gradient and inversely proportional to internal flow resistances. Therefore, relating the measured xylem water potentials to the transpiration rate as estimated by the ratio  $VPD/r_s$  (for non-stress conditions) indicates that flow resistances within the bog plants may be higher than in the upland ecotypes. The rapid decrease of xylem potential with the commencement of transpiration in the bog plants gives some measure of the magnitude of the driving force (water potential gradient) needed to move water through the plant in the presence of high internal resistance.

Assuming that there is no resistance to water movement in the saturated peat soil, the resistances indicated for these bog plants may be considered to lie between the root-soil interface and the stem xylem tissue just beneath the leaf layer (the point at which the xylem water potential was measured). It is believed that poor soil aeration, a condition typical of bogs (see, for example, Armstrong and Boatman, 1967), inhibits root absorption, but is this alone enough to account for the resistance indicated here? Studies of Macklon and Weatherley (1965) suggest that root resistance plays little part in establishing leaf water potentials lower than  $-5$  bars.

Flow resistances in the xylem, on the other hand, are generally considered to be the lowest in the soil-plant-atmosphere continuum. Increased resistance in the xylem may possibly result from decreased diameters of conducting elements or through the blocking of these by sclerids or tyloses, creating in effect a more tortuous translocation pathway in bog plants. Preliminary microscopic examination of the xylem tissue, however, showed vessel elements to be on the order of 15 to 25 microns in diameter, essentially the same as in the upland ecotypes and not small



enough to increase flow resistance, and revealed no obstructions in the vessels (Terrell Comstock, unpublished data). The source of the high internal flow resistances in bog plants, if indeed they exist, thus escapes recognition for the moment.

The values for VPD in this analysis were taken from the wet-bulb depression only (i.e., atmospheric VPD) which presupposes that the leaf and air were in thermal equilibrium. If leaf temperatures were elevated above air temperature, then the calculated values for  $VPD/r_s$  would be low. Presumably however, with all plants fully exposed, the direction of the error would be the same in all cases. Moreover, when it is considered that the water potential of the upland plants must also reflect flow resistances outside the plant, since it can be assumed that the soil adjacent to their roots is not saturated, then the relative differences in water potential levels seen here take on even greater significance with respect to indicated internal differences.

Of considerable interest in these data is the fact that the midday xylem potentials in the two *Gaylussacia* populations remained relatively close. This suggests the possibility of a closely regulated optimum water potential level for the species, indicating also very sensitive stomatal control, with the stomates of the upland plants closing before any detectable decrease in xylem water potential. This same phenomenon has been observed in yellow birch (C. A. Federer, personal communication) and is somewhat suggestive of the kind of direct response of stomates to evaporative conditions of the atmosphere, independent of leaf water potentials but conditioned by soil water supply, as reported by Schulze *et al.* (1972).

As for the question of xeromorphy in bog plants, leaf sclerophylly appears of advantage only insofar as it may be related to the evergreen habit, possibly preventing winter desiccation when water uptake is impaired. There is not enough evidence yet, however, to conclude that the water metabolism of bog plants is entirely similar to that of their upland counterparts. While Small (1972a) demonstrated



some similarity in the water status of woody plants in a bog and nearby mesic habitat, his mesic site was described as including a marsh and field adjacent to the bog and many of the species studied at that site, such as *Ilex verticillata* (L.) Gray, *Nemopanthus mucronata* (L.) Trel., and *Alnus rugosa* (DuRoi) Spreng. are typically confined to wetland areas. Lacking any data to the contrary, this suggests that the two environments may not have differed significantly in terms of soil-water availability. The data presented here indicate that dissimilarities in water metabolism between bog and upland ecotypes may indeed exist in relation to soil-water availability or other edaphic differences.

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